frontiers | Frontiers in Forests and Global Change

TYPE Original Research
PUBLISHED 08 August 2025
DOI 10.3389/ffgc.2025.1631614

OPEN ACCESS

EDITED BY
Daniel Moya,
University of Castilla-La Mancha, Spain

REVIEWED BY
Jorgelina Franzese,
National University of Comahue, Argentina
Víctor Fernández García,
Université de Lausanne, Switzerland

*CORRESPONDENCE
Andres Fuentes-Ramírez
✉ andres.fuentes@ufrontera.cl

RECEIVED 20 May 2025
ACCEPTED 28 July 2025
PUBLISHED 08 August 2025

CITATION
Diaz-Mons B, Arroyo-Vargas P, Vargas-Gaete R, Almonacid-Muñoz L, Herrera H and Fuentes-Ramírez A (2025) Resilience beyond expectations: seedling performance under fire and grazing pressure in old-growth Andean *Araucaria araucana* forests.
Front. For. Glob. Change 8:1631614.
doi: 10.3389/ffgc.2025.1631614

Resilience beyond expectations: seedling performance under fire and grazing pressure in old-growth Andean *Araucaria araucana* forests

Bernardita Diaz-Mons[1,2,3], Paola Arroyo-Vargas[1,3], Rodrigo Vargas-Gaete[1,3,4], Leonardo Almonacid-Muñoz[1,4], Héctor Herrera[1,4] and Andres Fuentes-Ramírez[1,3,4]*

[1]Departamento de Ciencias Forestales, Laboratorio de Ecosistemas y Bosques (EcoBos), Universidad de La Frontera, Temuco, Chile, [2]Programa de Magíster en Manejo de Recursos Naturales, Facultad de Ciencias Agropecuarias y Medioambiente, Universidad de La Frontera, Temuco, Chile, [3]Centro Nacional de Excelencia para la Industria de la Madera (CENAMAD), Pontificia Universidad Católica de Chile, Santiago, Chile, [4]Center for Biodiversity and Ecological Sustainability (C-BEST), Facultad de Ciencias Agropecuarias y Medioambiente, Universidad de La Frontera, Temuco, Chile

Altered fire regimes are mainly driven by anthropogenic factors and amplified by climate anomalies globally. Biological legacies that persist after fire are key for the post-fire vegetation recovery, facilitating the establishment and growth of new plant cohorts. However, these effects on long-lived conifers from southern South America still remains unclear. In this study, we experimentally evaluated the effect of biological legacies and cattle activity on seedling survival and growth of the conifer *Araucaria araucana* (monkey puzzle tree) in fire-affected forests in south-central Chile. Biological legacies in the burned areas included fallen logs, standing dead trees and understory canopy cover, which are hypothesized to have positive effects on seedling performance when facing harsh post-fire site conditions. These effects would be more beneficial within areas subjected to cattle activity after severe fires. *Araucaria araucana* seedlings were planted within burned forests affected with moderate and high fire severity, comparing both the presence and absence of post-fire biological legacies and cattle activity, and monitored for 5 years. Results revealed that the overall seedling survival rate was generally good, ranging from 79–83% in moderate and high fire severity, respectively. The effect of biological legacies on seedling survival was in general positive, but not significant across all conditions. We found a significant positive effect on plant height growth when biological legacies were nearby and when cattle were excluded, particularly in burned forests with high fire severity. Neither post-fire biological legacies nor cattle exclusion showed a positive effect on the number of new shoots or plant collar growth. In summary, *A. araucana* is well capable of surviving and growing in absence of biological legacies or when preventing cattle into burned areas, highlighting its great resilience capacity to recover after severe forest fires. Yet, these practices may benefit post-fire vegetation recovery in the long-term and could be considered when feasible.

KEYWORDS

Araucaria-Nothofagus **forests, seedling growth, survival, cattle impacts, post-fire restoration, wildfires, biological legacies**

Introduction

Fire regimes are experiencing major alterations globally due to the intensification and prolongation of fire seasons, increased occurrence and severity, as well as because anthropogenic effects of land use changes (Bowman et al., 2020; Kelly et al., 2023; Sayedi et al., 2024). Although fire is a natural disturbance that can act as a shaping agent in several ecosystems, there is growing concern about the effect on temperate forests less adapted to fires, since drier and warmer climatic conditions are catalyzing more severe and/or recurrent fires (Enright et al., 2015; Johnstone et al., 2016). As an example, burn areas in temperate forests of South America have increased by 17% annually, with a significant intensify in burn severity of 3.5% per year (Fernández-García and Alonso-González, 2023). In this context, the role of post-fire biological legacies, such as surviving trees, downed logs or understory canopy cover, in facilitating forest recovery and mitigating the negative effects of fire has become increasingly recognized (Franklin et al., 2000; Lindenmayer et al., 2019).

Plant species in fire-prone ecosystems that have co-evolved with more frequent fires often exhibit different functional traits that allow them to survive and/or quickly reestablish after fire (He et al., 2019; Vargas-Gaete et al., 2024). Functional and structural traits such as serotinous cones (seed protection from heat), thick bark (protection of living tissues: vascular cambium), shedding of lower branches (reduced vertical connectivity), apical, epicormic or underground resprouting (rapid species colonization), among others, confer to species the ability to persist after fire (Pausas et al., 2004; Keeley et al., 2011; Rodman et al., 2020). Conversely, ecosystems that have co-evolved with less fire pressure are characterized by a predominance of fire-sensitive species, i.e., species with functional traits less tolerant to a more frequent and/or severe fire regime (Whitlock et al., 2015; Tepley et al., 2018). Despite these adaptive responses, as well as the state of biotic factors that persist after a wildfire and facilitate the establishment of new cohorts (i.e., presence of biological legacies), the recruitment, growth, and ultimately the survival of species could be at risk in the face of altered fire regimes (Enright et al., 2015; Johnstone et al., 2016). Additionally, the post-fire effects of herbivore browsing and trampling (i.e., cattle use by local communities) can exacerbate the negative effects solely attributed to fire, hindering proper forest recovery (Raffaele et al., 2011; Lewis et al., 2024).

Southern temperate forests in southern South America are predominantly characterized by a mixed or low-frequency fire regime, with most of the forest dominated by tree species sensitive to fire. However, a smaller proportion of tree species possess the ability to resprout or withstand low-to-moderate fire intensities (Beard, 1990; Whitlock et al., 2015; Kitzberger et al., 2016). Mixed temperate forests dominated by *Araucaria araucana* (Mol.) K. Koch and *Nothofagus* spp. in the Andean region of Chile and Argentina (henceforth referred to as *Araucaria-Nothofagus* forests) are composed of species with varying levels of fire tolerance. Some species are highly susceptible to fire due to thin bark [e.g., *Nothofagus dombeyi* (Mirb.) Oerst., *N. pumilio* (Poepp. & Endl.) Krasser], while others exhibit adaptations such as thick bark and shedding of lower branches or the ability to resprout rapidly after fire (e.g., *Araucaria araucana*; Veblen, 1982; Burns, 1993; González et al., 2010; Arroyo-Vargas et al., 2024). This suggests that fire has been rather infrequent in these forests, generally with low-to-moderate severity (González et al., 2010; Fuentes-Ramirez et al., 2022). However, changes in fire frequency and severity in recent decades may indicate a shift in the fire regime of these ecosystems (González et al., 2020; McWethy et al., 2018). Furthermore, the introduction of agriculture and livestock in the early 18th century, which was intensified from the 1750s onwards, led to the use of fire to clear forest and habilitate land for these practices by Pehuenche communities, altering the historical fire regimes in forests dominated by *A. araucana* (Torrejón, 2001; González et al., 2020). Moreover, in Andean ecosystems, with the presence of seasonal winter and summer pastures, practices such as cattle transhumance have been carried out for centuries in these areas until the present day, even within areas affected by fire (Marchant, 2019). Therefore, the combined effects of more frequent fires and cattle herbivory may have significantly affected the survival and growth of tree species, posing a serious threat to the long-term recovery of burned forests (Arroyo-Vargas et al., 2024).

The slow-growing southern South American endemic conifer *A. araucana* is distributed between 37° and 40° S, mostly in the Andean region of central-south Chile and Argentina (Veblen, 1982; Sanguinetti et al., 2023). The species is currently protected under CITES by Chile and Argentina, and it is listed as endangered by the IUCN (Convention on International Trade in Endangered Species, 2001; Premoli et al., 2011). Moreover, the species holds significant ecological and cultural importance by local Pehuenche communities (Rozzi et al., 2012). Although *A. araucana* possesses traits that allow it to survive low-to-moderate severity fires (e.g., development of thick bark, shedding of lower branches in mature individuals, development of female cones in the upper crown; Burns, 1993), under severe and frequent fires, its mortality rate is practically 100% (Assal et al., 2018; Franco et al., 2022; Arroyo-Vargas et al., 2024). Additionally, *A. araucana* populations have declined by 50% from their original estimated distribution of 500,000 ha, largely due to selective logging for its valuable timber during the first half of the 20th century (Lara et al., 1999). In recent years, anthropogenic wildfires, cattle impacts, and an unsustainable harvest of its edible seeds have further exacerbated the situation (González et al., 2020; Donoso et al., 2024). This combination of pressures has raised significant concerns about the species' ability to recover after severe fire events. Moreover, the importance of *A. araucana* in the territory and local communities from its evolutionary, biological and sociocultural perspective makes the species a key component of the ecosystems where it occurs (Rozzi et al., 2012; Sanguinetti et al., 2023).

As fire generally burns in a patchy manner, post-fire biological legacies that remain in the forest are thought to be crucial for facilitating seedling establishment, survival and growth over time (Turner et al., 1998; Seidl et al., 2014). These biological legacies may include surviving trees, downed logs or understory canopy cover. Moreover, the presence of herbivores [e.g., cattle (*Bos taurus*)] in burned areas greatly challenge the resilience of these forests and its ability to regenerate (Sanguinetti and Kitzberger, 2010; Zamorano-Elgueta et al., 2012; Arroyo-Vargas et al., 2019). In this context, restoration efforts are essential, and their success will depend on the interplay between the effects of fires, grazing pressure and the presence of biological legacies. These legacies provide essential advantages to seedlings, including shade, protection, and enhanced micro-habitats (Franklin et al., 2000; Rudolphi et al., 2014; Ferreiro et al., 2018). Currently, it is unclear how this interplay may affect the establishment of *A. araucana* seedlings in old-growth forests severely burned in the

 10.3389/ffgc.2025.1631614

short-term. Thus, our study is specifically designed to answer the following questions:

(i) How does fire severity influence survival patterns of *A. araucana* seedlings in the presence of biological legacies and under cattle exclusion?, and (ii) How do the presence of biological legacies and cattle grazing affect the growth rate of *A. araucana* seedlings in different post-fire severity levels? We hypothesized that the presence of post-fire biological legacies and the exclusion of cattle lead to an increased survival and growth of Araucaria seedlings, especially in areas of high fire severity.

Understanding the complex interactions between fire, seedling survival and initial growth is crucial for designing more effective forest management and better conservation practices to canalize restoration efforts of this ancient, iconic forests in the Andean region of southern South America.

Methods

Study site and species

The study area is located in Andean old-growth forests of *Araucaria araucana*, within a protected area in La Araucanía Region, south-central Chile between 800 and 1,400 m a.s.l. (38°S, 71°W, Figure 1). The climate is temperate, with a dry and warm summer season from December to March, and a humid (i.e., with ice and snow) in winter and spring (Luebert and Pliscoff, 2017), with an annual mean precipitation of 1,380 mm (period between 1993–2023). The maximum mean temperature in summer is 21.8°C, while the minimum mean temperature in winter is 4°C (period between 1993–2023). Soils are formed from volcanic ash, with moderate depth, dark brown color, coarse texture, and good permeability (Flores et al., 2010). Vegetation is formed by temperate deciduous forests, with tree dominance of *A. araucana* (araucaria) and *N. pumilio* (lenga). The understory is represented by *Alstroemeria aurea*, *Chusquea culeou*, *Berberis microphylla*, and *Gaultheria poepiggi* (Urrutia-Estrada et al., 2018; Arroyo-Vargas et al., 2019).

The dominant species in these forests is *A. araucana*, which is a native conifer, with populations occurring primarily in the Andean region of southern Chile and to a lesser extent in Argentina (Veblen, 1982). It is a slow-growing tree that can reach heights of up to 50 m, with a diameter exceeding 2 m and a lifespan of over 1,000 years (Veblen, 1982; Burns, 1993; González et al., 2006; Aguilera-Betti et al., 2017). The species is characterized by developing a bark up to 20 cm thick in adult individuals, self-pruning of its lower branches giving it a typical umbrella shape, forming cones at the top of the crown, possessing latent growth buds under the bark (i.e., epicormic shoots)

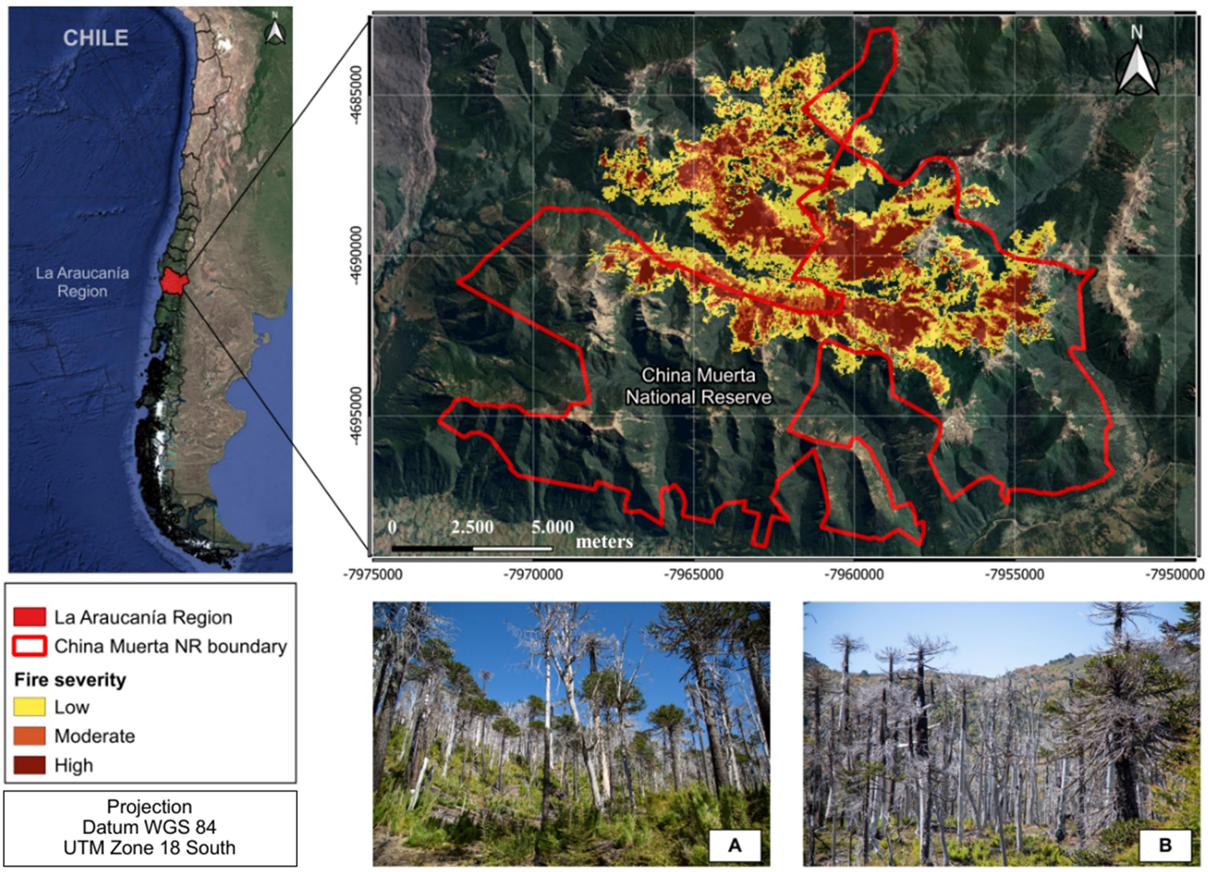

FIGURE 1
Map of the study area in National Reserve China Muerta, south-central Andes of Chile, which was affected by a mixed-severity forest fire in 2015. **(A)** Shows areas of moderate severity. **(B)** Areas of high fire severity in which the experimental planting of *A. araucana* seedlings was conducted.

that can resprout after low-to-moderate fires (Veblen, 1982; Burns, 1993; González et al., 2006).

Forest fire description

The forest was affected by a wildfire accidentally ignited by human activity in 2015 (March–April), affecting approximately 3,750 ha (Mora and Crisóstomo, 2016). The fire primarily damaged forests dominated by *A. araucana*. This wildfire spread rapidly facilitated by a mega-drought that affected central-southern Chile since 2010 and high summer temperatures prior to the fire (Garreaud et al., 2017; McWethy et al., 2018). The fire was of mixed severity (Fuentes-Ramirez et al., 2020), damaging the forest with low (i.e., surface fire, greater damage to the understory), moderate (i.e., partially burned trees, canopy with living and dead trees; Figure 1A), and high severity (i.e., completely charred canopy and understory; Figure 1B). Burn severity assessment of the study area was previously conducted by Mora and Crisóstomo (2016), performing the delta normalized burn ratio (dNBR) analysis, using pre-fire and post-fire Landsat imagery (Miller and Thode, 2007). Groundtruthing was conducted afterwards to specifically define areas of moderate and high fire severity (Fuentes-Ramirez et al., 2018). In areas of high fire severity, trees and understory vegetation were completely charred. There were less than 1% of canopy trees that survived fire in high-severity fire zones. In moderate fire severity areas, trees were partially burned, the forest canopy presented some unburned branches, and there was understory vegetation that survived fire. As a result, we defined moderate-severity areas as areas where 50% of canopy trees survive. Within these burned areas, cattle is the major disturbance agent in the reserve due to the historical (and current) use by Pehuenche communities. Although there is no official record of the number of heads that graze in the area, unofficial estimates approximate to 50–60 cattle heads per season, which is fairly high for a relatively small area where our study took place (ca. 60 ha; Arroyo-Vargas et al., 2019).

Study design and data collection

In a previous study conducted by Fuentes-Ramirez et al. (2019), 200 *A. araucana* seedlings were produced in the greenhouse, aimed for planting them in burned areas as a reforestation trial. Prior to planting, these seedlings were transferred to conditions similar to the study site, where they were acclimatized for 2 years. Subsequently, plants were randomly shuffled and planted in April 2019 within areas affected by the 2015 fire, and under two conditions: moderate and high fire severity. Within each of these conditions, the presence/absence of nearby biological legacies (i.e., fallen or standing dead trees, understory canopy), and areas with and without cattle exclusion were also considered (Table 1 and Figure 2). Thus, the full factorial design in our experiment included two levels of fire severity, two conditions of biological legacies and two conditions of cattle exclusion, where 25 Araucaria seedling were established within each combination (i.e., $2 \times 2 \times 2 \times 25 = 200$ experimental units). For cattle exclusion, we used permanently-fenced 10×10 m plots that were previously established in the summer of 2017 to evaluate the effect of browsing and trampling on post-fire regeneration of the vegetation (Arroyo-Vargas et al., 2019). As a second step, we identified post-fire biological legacies that consisted of fallen logs, dead trees, and understory canopy cover within and outside the exclusions, where seedlings were established at 50 cm from. Presence of biological legacies was visually assessed and defined within a 10×10m plot. Once planted, each seedling was tallied with a unique code using metal tags. The planting scheme consisted in 25 seedlings randomly shuffled within each study condition, considering a distance of 1.5 m between each individual. This was done following the natural way in which *A. araucana* seedlings establish, close to seed trees due to the limited dispersal of their seeds as a consequence of their size and weight (Fajardo and González, 2009; Fuentes-Ramirez et al., 2019). Seedlings were monitored at 6, 24, 48, 54 and 60 months after planting. Initially it was stipulated to sample every 6 months, but this was interrupted between 2020 and 2021 due to health and mobility restrictions associated with COVID-19 pandemic. Individual survival (i.e., alive or dead) was recorded, and seedling growth was measured in terms of total height (in cm) and number of new shoots. From 2022 onwards, the collar diameter (CD) of each seedling was also recorded.

TABLE 1 Planting design of *Araucaria araucana* seedlings in burned areas with moderate and high severity in the China Muerta National Reserve, south-central Chile.

Fire severity	Presence of biological legacies	Cattle exclusion	No. of seedlings
Moderate	No	No	25
		Yes	25
	Yes	No	25
		Yes	25
High	No	No	25
		Yes	25
	Yes	No	25
		Yes	25

Twenty five Araucaria seedlings were planted within each of the eight treatments for full factorial combination of fire severity, biological legacies and cattle exclusion, totaling 200 sampling units.

Statistical analysis

To analyze seedlings survival under different fire severity conditions, biological legacy effects, and cattle exclusion, we used the "*survival*" package (Therneau et al., 2024) implemented in the R software. The Kaplan–Meier method, a non-parametric maximum likelihood estimation (MLE), was used to estimate survival curves over time. Additionally, the log-rank test was employed to compare survival among different study conditions. A Cox proportional hazards model was also fitted, allowing us to model survival as a function of different predictor variables (i.e., severity, biological legacies, cattle) using the "*survminer*" package (Kassambara et al., 2021).

To assess seedling growth, we considered the variables total height, number of shoots, and root collar diameter as a function of fire severity, presence/absence of biological legacies, and cattle exclusion. Generalized linear mixed models (GLMMs) were fitted using the "*lme4*" package (Bates et al., 2015) in R. Fire severity (i.e., moderate vs. high), biological legacies (i.e., presence vs. absence), and cattle (i.e.,

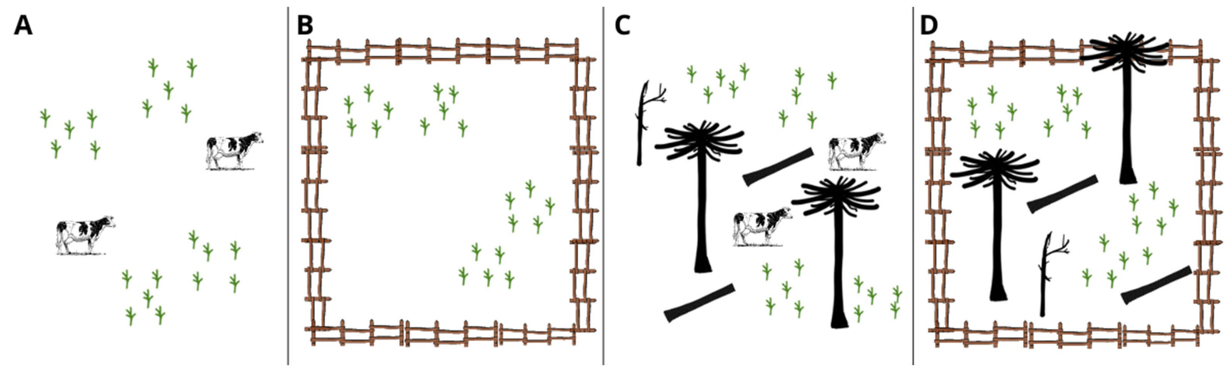

FIGURE 2
Scheme of experimental planting design of *A. araucana* seedlings considering two fire severity levels (moderate and high) and four study conditions. **(A)** Areas without cattle exclusion and without biological legacies. **(B)** Areas with cattle exclusion and without biological legacies. **(C)** Areas without cattle exclusion and with presence of biological legacies. **(D)** Areas with cattle exclusion and with biological legacies.

with and without exclusion) were considered fixed effects predictors, while plant individuals were the random factor. The normality and homoscedasticity of the data were assessed using the Shapiro–Wilk and Levene tests, respectively implemented in R (R Core Team, 2024). To evaluate and compare models, we used the Akaike information criterion (AIC). Additionally, marginal R^2 and conditional R^2 were considered to identify the proportion of variance explained by fixed effects and the combination of fixed and random effects, respectively.

Results

Araucaria seedling survival

From an initial number of 200 Araucaria seedlings planted at moderate and high burn severity sites (i.e., 100 seedlings planted in each fire condition), a total of 159 seedlings survived after 60 months of assessment, with an overall survival rate of 79.4%. The survival rates at moderate and high fire severity conditions were 75.6% (76 seedlings) and 83.3% (83 seedlings), respectively, showing no statistical difference after 60 months of planting ($\chi^2 = 1.8, p > 0.18$). At moderate fire severity sites, seedling survival rate was higher in areas with presence of biological legacies and without cattle exclusion (85%; Table 2 and Figure 3), while at high fire severity sites, survival rate was higher with cattle exclusion and both with and without biological legacies (90%; Table 2 and Figure 3). However, we found no statistical differences in the probability of survival of Araucaria seedlings based on the presence or absence of biological legacies, cattle exclusion or fire severity levels, indicating that survival of *A. araucana* is primarily determined by individual traits rather than post-fire conditions (Table 2).

Araucaria seedling growth

Neither biological legacies nor cattle exclusion showed significant effects on seedlings' height in areas affected by moderate burn severity over time (Figure 4A). During the five-year period, *A. araucana* seedlings averaged 20 cm in height, growing at a mean rate of 3.2 cm annually. The absence of biological legacies, however, caused a significantly greater number of buds ($p \leq 0.024$, Figure 4C) and diameter at root collar ($p \leq 0.001$, Figure 4E) from month 24 and 48 in areas affected by the same fire severity, respectively. In contrast, cattle exclusion did not cause any statistical difference on growth variables. Within forests affected with high burn severity, we found that the presence of biological legacies and cattle exclusion were associated with greater growth in height in months 24 and 48 for the former ($p \leq 0.049$, Figure 4B), and month 6 and 24 for the latter ($p \leq 0.013$, Figure 4B), respectively. The number of buds in Araucaria seedlings was significantly greater in plots without biological legacy in month 54 ($p = 0.031$, Figure 4D), and without cattle exclusion in the same month ($p = 0.044$, Figure 4D). Lastly, significantly greater growth on diameter at root collar was detected without biological legacy in month 54 ($p = 0.033$, Figure 4F), and without cattle exclusion from month 54 ($p \leq 0.039$, Figure 4F) in areas burned with high fire severity. The results (which are highly variable) also emphasize the importance of individual characteristics when predicting growth patterns after fire.

Overall, fitted generalized linear mixed models showed that regardless of the presence of biological legacies or cattle, Araucaria seedlings were well capable to survive and grow in burned areas. At moderate fire severity sites, seedling height was significantly greater when cattle was excluded, while the number of buds and root collar diameter were significantly influenced by biological legacies (Supplementary material 1). At high fire severity sites, both height and root collar diameter were significantly greater under cattle exclusion, whereas the number of buds was strongly affected by biological legacies (Supplementary material 2). Overall, the contribution of biological legacies and cattle exclusion (i.e., fixed effects) were low (marginal $R^2 \sim 1\%$), but the addition of random effects significantly improved model performance (conditional $R^2 = 32\%$). This reflects that individual features of the species (rather than site conditions) play a more significant role in determining Araucaria's survival and growth patterns in burned areas.

Discussion

After 5 years of monitoring in the field, the survival trial of planted seedlings of *A. araucana* within burned areas did not exhibit

TABLE 2 Probability of survival in accordance with the presence/absence of biological legacies and cattle exclusion-type of treatments follows the combination of these.

Fire severity	Biological legacies	Cattle exclusion	Treatment	Number of seedlings	Survival rate	Log-rank χ^2 (p-value)
Moderate and high together	No	No	Type A	60	0.717	1.8 (0.38)
		Yes	Type B	40	0.850	
	Yes	No	Type C	40	0.850	
		Yes	Type D	40	0.800	
Moderate	No	No	Type A	30	0.700	2.0 (0.58)
		Yes	Type B	20	0.800	
	Yes	No	Type C	20	0.850	
		Yes	Type D	20	0.700	
High	No	No	Type A	30	0.733	3.9 (0.27)
		Yes	Type B	20	0.900	
	Yes	No	Type C	20	0.850	
		Yes	Type D	20	0.900	

The log-rank test statistics and p-values are informed. Treatment disclosure: Type A, without biological legacy/without cattle exclusion. Type B, without biological legacy/with cattle exclusion. Type C, with biological legacy/without cattle exclusion. Type D, with biological legacy/with cattle exclusion.

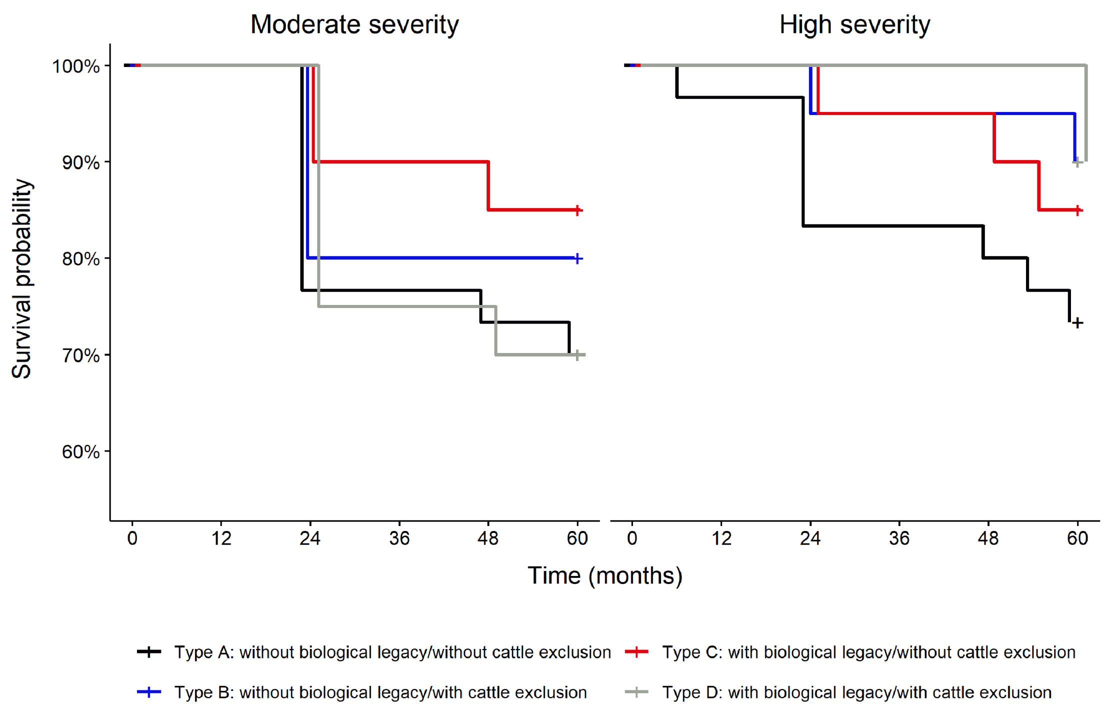

FIGURE 3
Survival probability plots using the Kaplan–Meier estimates of survival function for *Araucaria araucana* seedlings at moderate (left) and high (right) burn severity sites. Treatment types are represented according to Table 2. The x-axis represents the time in years, and y-axis the survival probability.

significant differences across treatments (e.g., with vs. without biological legacies or with cattle exclusion) in areas affected by moderate and high fire severities. The survival rate reported in this research fluctuated between 72 and 85% across all the study conditions, which is considered quite good. A similar study of *A. araucana* seedlings, conducted in areas with no burns or biological legacies, found no significant differences in seedling survival comparing areas with and without cattle exclusion (Rechene et al., 2003). However, other studies on conifers have shown that seedling mortality rates can vary widely depending on the species, fire severity, post-fire conditions, climate, and/or site-level topographic conditions (Marsh et al., 2022; Andrus et al., 2022; Marshall et al., 2024). For example, in boreal forests, species like black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*), often exhibit serotiny, a reproductive strategy that ensures seed dormancy until triggered by fire (Keeley et al., 2011). This adaptation provides a reliable seed bank for post-fire

10.3389/ffgc.2025.1631614

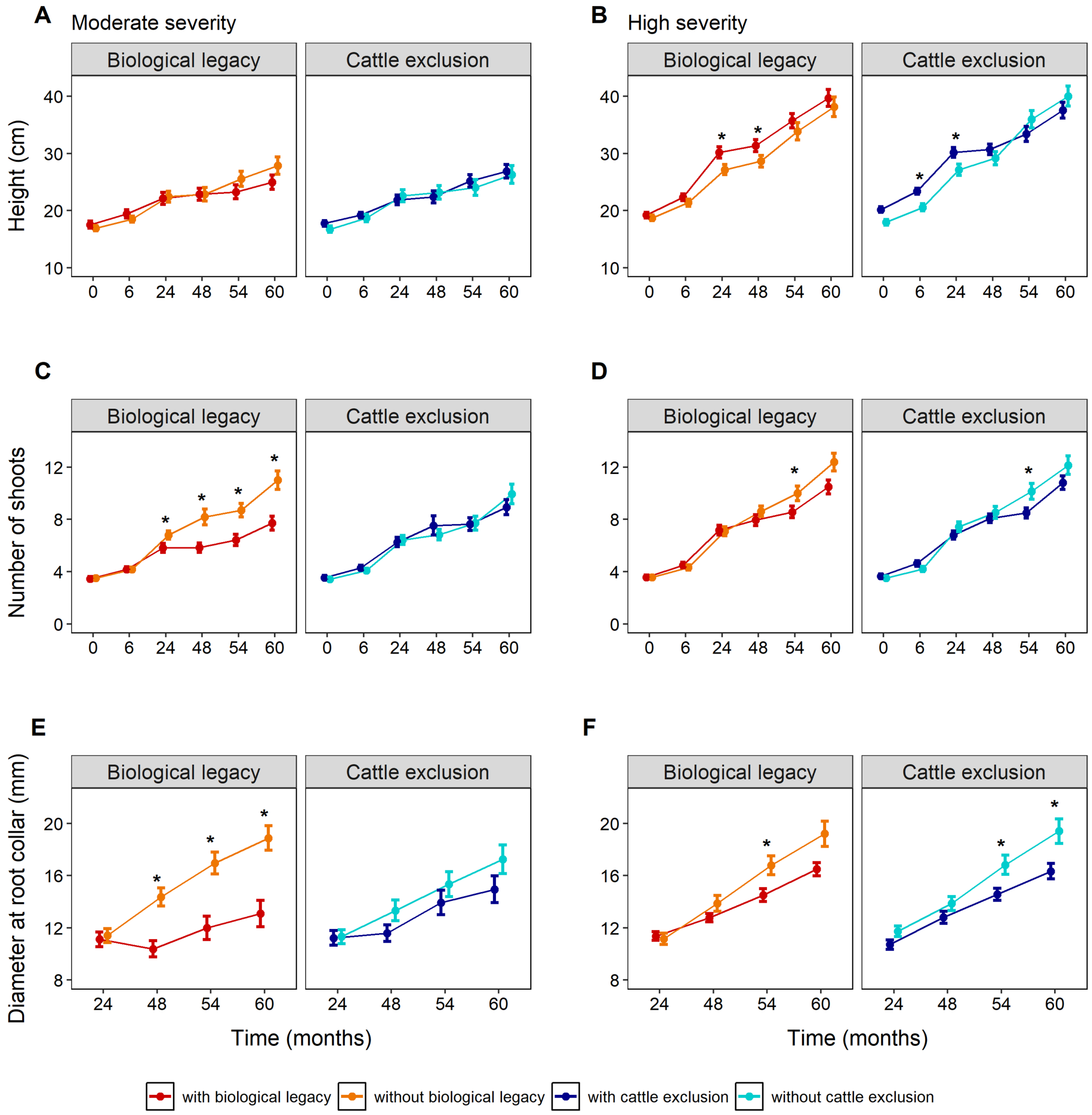

FIGURE 4
Mean growth in terms of height (cm), number of buds, and diameter at root collar (mm) of *Araucaria araucana* seedlings planted in areas burned with moderate **(A,C,E)** and high **(B,D,F)** fire severity over time (i.e., 5 years). Error bars represent standard errors, and asterisks indicate significant differences ($p < 0.05$) between growths measured within each period of time.

regeneration, but even serotinous species can experience high mortality rates if fires are too severe or frequent over time (Brown and Johnstone, 2012; Buma et al., 2013; Harvey et al., 2016; Turner et al., 2019). In contrast, many coniferous species in temperate forests of the southern hemisphere, including *A. araucana*, rely on dispersed seeds and post-fire seed germination, which is generally high for Araucaria (Fuentes-Ramirez et al., 2019). On this basis, biological legacies (i.e., fallen trees or standing snags) are thought to be important for improving post-fire site conditions at the micro-site scale by providing shelter and protection especially for the establishment of new seedlings after disturbances that may increase survival (Franklin et al., 2000; Arroyo-Vargas et al., 2019; Lindenmayer et al., 2019). What might explain why *Araucaria araucana* seedlings are able to survive well in burned areas with no aid of biological legacies, is the attribute of activating physiological mechanisms that allow them to tolerate short-term droughts (Papú et al., 2021), which is related to high survival rate even though post-fire biological legacies were absent.

The growth of seedlings in terms of height was constant over time independently of the treatment (i.e., with vs. without biological legacies or with cattle exclusion) and burn condition (i.e., moderate or high fire severity). Although there were some significant differences in growth after 24- or 54-months post-plantation, the fitted models did not show a significantly better performance when considering any of the explanatory variables (biological legacies or absence of cattle activity). Nonetheless, number of shoots and diameter at root collar of seedlings showed a trend of improving when biological legacies were absent instead. On a previous study, Rechene et al. (2003) also measured diameter at root collar and height of *A. araucana* seedlings that were planted in the field with and without exclusions. However, they only found statistical differences in the growth of the diameter at root collar between seedling groups with different years when planted in the field, which is expected. Nonetheless, seedling survival can be low because of herbivory, trampling, competition with weeds, and an increase in the severity and frequency of fires in burned areas (Sanguinetti and Kitzberger, 2010; Crovo et al., 2021; Lewis et al., 2024). In addition, our study only considers the early establishment of seedlings in a period of 5-years, and longer measurements are needed to better understand plant growth and the potential long-term effects of biological legacies and cattle exclusion in a long-lived conifer such as *A. araucana*. In this context, a wide range of studies have demonstrated that the presence of biological legacies and the exclusion of cattle improve the performance of seedling establishment of *A. araucana* from temperate forests in southern hemisphere (González and Veblen, 2007; Blackhall et al., 2008; Zamorano-Elgueta et al., 2012), which can ensure the success of seedling establishment in harsh conditions when the forest is subjected to disturbances. Nonetheless, these findings are seldom taken into account when restoration actions are designed or implemented at larger operational scales (Stanturf et al., 2014; Köbel et al., 2021). Despite these practice challenges, our results highlight the remarkable resilience of *A. araucana* in burned forests, demonstrating its ability to survive and grow even under the harsh challenging conditions imposed by severe anthropogenic fire events, presenting a significant opportunity to tackle down restoration bottlenecks and support ecosystem recovery more efficiently (Bannister et al., 2018).

Our study shows that while *A. araucana* can establish in burned areas, its slow early growth as a seedling may be affected by predicted warmer and drier conditions. In addition, shifts from natural successional trajectories may be exacerbated by the combined effects of fire severity, cattle pressure, and other disturbances, highlighting the need for strategic restoration actions to support ecosystem recovery (Bannister et al., 2022; Donoso et al., 2024). Furthermore, and despite harsh post-fire conditions in burned areas, *A. araucana* displays key evolutionary characteristics that allow it to survive and grow well without biological legacies or under cattle exclusion management, which would make it easier for restoration efforts to be undertaken at broader scales.

Restoration implications

The results show that planted *A. araucana* seedlings exhibit high survival rate and good initial height growth during the first 5 years post-fire, which could be auspicious for post-fire restoration plans. One of the main issues on these forests is that severe wildfires importantly affect the natural regeneration of *A. araucana* due to the lack of surviving female trees in burned patches (Arroyo-Vargas et al., 2024). Although the species has some fire adaptations (Burns, 1993; González et al., 2006), the mortality of mature trees is high in large severely burned areas, and seedling establishment is practically absent within these burned patches (Arroyo-Vargas et al., 2024; Assal et al., 2018; González et al., 2010). Our study reports that *A. araucana* is well capable of surviving and growing with no specific management, such as using biological legacies as protection or preventing cattle into burned areas. Considering these results and previous studies, when planning planting programs and management, large areas affected by severe fires should be prioritized for restoration due to the lack of natural regeneration. Thus, using nearby biological legacies does not appear to increase seedling establishment in the short-term, nor does avoiding cattle in burned areas. Yet, these practices may benefit post-fire vegetation recovery in the long run (Arroyo-Vargas et al., 2019; Blackhall et al., 2008; Zamorano-Elgueta et al., 2012), and could be considered when feasible.

Conclusion

Survival of Araucaria seedlings reached an overall rate of 75% after 5 years of assessment, with no significant effects of biological legacies nor the exclusion of cattle. Neither of the fire severity conditions assessed in this research had an effect on seedling survival over time. Thus, in absence of further disturbances, seedling survival with no improved micro-site conditions caused by biological legacies, would be enough to properly recover Araucaria after fires. Plant growth did show a significant and positive response only for height in areas of high fire severity when seedlings were planted nearby biological legacies and were protected from cattle. This, however, was marked in the first 2 years post-planting, and then the effect tended to weaken as plants grew over time. Furthermore, these findings were not consistent for other growth variables such as number of buds nor for root collar diameter. In summary, *A. araucana* is well capable of surviving and growing in absence of biological legacies or when preventing cattle into burned areas, highlighting a great resilience capacity that exceeds expectations under fire and grazing pressure to face its recovery after severe forest fires.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

BD-M: Data curation, Formal analysis, Writing – original draft. PA-V: Supervision, Writing – review & editing, Validation, Visualization. RV-G: Writing – review & editing, Conceptualization, Methodology, Resources. LA-M: Writing – review & editing, Visualization. HH: Visualization, Writing – review & editing. AF-R: Writing – review & editing, Conceptualization, Funding acquisition, Project administration, Resources, Supervision.

Funding

The author(s) declare that financial support was received for the research and/or publication of this article. This research was funded by ANID FONDECYT Regular 1241295 (PI A. Fuentes-Ramirez). AF-R thanks to DIUFRO PP24-0015, Dirección de Investigación, Universidad de La Frontera. AF-R, BD-M, PA-V, and RV-G thank the support received from Centro ANID Basal CENAMAD (FB210015). HH thanks to ANID FONDEF ID23I10303 and RV-G thanks DIUFRO DI22-0042. This research is part of the Red Firewall initiative (ANID FOVI 220101 and Grant ANID AMSUD 240053).

Acknowledgments

The authors thank several students as well as the park rangers from the National Reserve China Muerta for helping with fieldwork. O. Barra and Z. Calzadilla assisted with greenhouse work. Two reviewers made a number of comments and suggestions greatly improving the first version of the manuscript.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Generative AI statement

The authors declare that Gen AI was used in the creation of this manuscript. During the preparation of this work the author(s) used the DeepL App in order to improve language and readability. After using this tool/service, the author(s) reviewed and edited the content as needed and take(s) full responsibility for the content of the publication.

Publisher's note

All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2025.1631614/full#supplementary-material

References

Aguilera-Betti, I., Muñoz, A. A., Stahle, D., Figueroa, G., Duarte, F., González-Reyes, Á., et al. (2017). The first millennium-age *Araucaria araucana* Patagonia. *Tree-Ring Res.* 73, 53–56. doi: 10.3959/1536-1098-73.1.53

Andrus, R. A., Droske, C. A., Franz, M. C., Hudak, A. T., Lentile, L. B., Lewis, S. A., et al. (2022). Spatial and temporal drivers of post-fire tree establishment and height growth in a managed forest landscape. *Fire Ecol.* 18:29. doi: 10.1186/s42408-022-00153-4

Arroyo-Vargas, P., Busby, S., Veblen, T. T., González, M. E., and Holz, A. (2024). Impacts of a short-interval severe fire on forest structure and regeneration in a temperate Andean *Araucaria-Nothofagus* forest. *Fire Ecol.* 20:93. doi: 10.1186/s42408-024-00327-2

Arroyo-Vargas, P., Fuentes-Ramírez, A., Muys, B., and Pauchard, A. (2019). Impacts of fire severity and cattle grazing on early plant dynamics in old-growth *Araucaria-Nothofagus* forests. *For. Ecosyst.* 6:44. doi: 10.1186/s40663-019-0202-2

Assal, T. J., González, M. E., and Sibold, J. S. (2018). Burn severity controls on postfire *Araucaria-Nothofagus* regeneration in the Andean Cordillera. *J. Biogeogr.* 45, 2483–2494. doi: 10.1111/jbi.13428

Bannister, J. R., Nelson, C. R., and Holz, A. (2022). "Conceptos y bases ecológicas para la restauración de ecosistemas forestales" in Restauración de Ecosistemas Forestales (Santiago: Editorial Universitaria).

Bannister, J. R., Vargas-Gaete, R., Ovalle, J. F., Acevedo, M., Fuentes-Ramirez, A., Donoso, P. J., et al. (2018). Major bottlenecks for the restoration of natural forests in Chile. *Restor. Ecol.* 26, 1039–1044. doi: 10.1111/rec.12880

Bates, D., Mächler, M., Bolker, B., and Walker, S. (2015). Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67, 1–48. doi: 10.18637/jss.v067.i01

Beard, J. S. (1990). Temperate forests of southern hemisphere. *Vegetatio* 89, 7–10. doi: 10.1007/BF00134430

Blackhall, M., Raffaele, E., and Veblen, T. T. (2008). Cattle affect early post-fire regeneration in a *Nothofagus dombeyi-Austrocedrus chilensis* mixed forest in northern Patagonia, Argentina. *Biol. Conserv.* 141, 2251–2261. doi: 10.1016/j.biocon.2008.06.016

Bowman, D. M. J. S., Kolden, C. A., Abatzoglou, J. T., Johnston, F. H., van der Werf, G. R., and Flannigan, M. (2020). Vegetation fires in the anthropocene. *Nat. Rev. Earth Environ.* 1, 500–515. doi: 10.1038/s43017-020-0085-3

Brown, C. D., and Johnstone, J. F. (2012). Once burned, twice shy: repeat fires reduce seed availability and alter substrate constraints on *Picea mariana* regeneration. *For. Ecol. Manag.* 266, 34–41. doi: 10.1016/j.foreco.2011.11.006

Buma, B., Brown, C., Donato, D., Fontaine, J., and Johnstone, J. (2013). The impacts of changing disturbance regimes on serotinous plant populations and communities. *Bioscience* 63, 866–876. doi: 10.1525/bio.2013.63.11.5

Burns, B. R. (1993). Fire-induced dynamics of *Araucaria araucana-Nothofagus antarctica* forest in the southern Andes. *J. Biogeogr.* 20, 669–685. doi: 10.2307/2845522

Convention on International Trade in Endangered Species (2001). Wild fauna and flora: *Araucaria araucana*. doi: 10.4067/S0717-92002015000100006

Crovo, O., Aburto, F., da Costa-Reidel, C., Montecino, F., and Rodríguez, R. (2021). Effects of livestock grazing on soil health and recovery of a degraded Andean araucaria forest. *Land Degrad. Dev.* 32, 4907–4919. doi: 10.1002/ldr.4079

Donoso, S., Peña-Rojas, K., Espinoza, C., Badaracco, C., Santelices-Moya, R., and Cabrera-Ariza, A. (2024). Reproductive patterns in *Araucaria araucana* forests in the Andean range, Chile. *Ecol. Process.* 13:19. doi: 10.1186/s13717-024-00497-6

Enright, N. J., Fontaine, J. B., Bowman, D. M., Bradstock, R. S., and Williams, R. J. (2015). Interval squeeze: altered fire regimes and demographic responses interact to threaten woody species persistence as climate changes. *Front. Ecol. Environ.* 13, 265–272. doi: 10.1890/140231

Fajardo, A., and González, M. E. (2009). Replacement patterns and species coexistence in an Andean *Araucaria-Nothofagus* forest. *J. Veg. Sci.* 20, 1176–1190. doi: 10.1111/j.1654-1103.2009.01117.x

Fernández-García, V., and Alonso-González, E. (2023). Global patterns and dynamics of burned area and burn severity. *Remote Sens.* 15:3401. doi: 10.3390/rs15133401

Ferreiro, N., Satti, P., and Mazzarino, M. (2018). Biological legacies promote succession and soil development on tephra from the Puyehue-Cordon Caulle eruption (2011). *Austral. Ecol.* 43, 435–446. doi: 10.1111/aec.12580

Flores, J. P., Espinosa, M., Martínez, E., Henríquez, G., Avendaño, P., Torres, P., et al. (2010). Determinación de la erosión actual y potencial de los suelos de Chile. (Pub. CIREN No. 139). Available online at: https://bibliotecadigital.ciren.cl/handle/20.500.13082/2016 (Accessed January 10, 2025)

Franco, M. G., Mundo, I. A., and Veblen, T. T. (2022). Burn severity in *Araucaria araucana* forests of northern Patagonia: tree mortality scales up to burn severity at plot scale, mediated by topography and climatic context. *Plant Ecol.* 223, 811–828. doi: 10.1007/s11258-022-01241-w

Franklin, J. F., Lindenmayer, D., MacMahon, J. A., McKee, A., Magnuson, J., Perry, D. A., et al. (2000). Threads of continuity. *Conserv. Pract.* 1, 8–17. doi: 10.1111/j.1526-4629.2000.tb00155.x

Fuentes-Ramirez, A., Almonacid-Muñoz, L., Muñoz-Gómez, N., and Moloney, K. A. (2022). Spatio-temporal variation in soil nutrients and plant recovery across a fire-severity gradient in old-growth *Araucaria-Nothofagus* forests of South-Central Chile. *Forests* 13:448. doi: 10.3390/f13030448

Fuentes-Ramirez, A., Arroyo-Vargas, P., Del Fierro, A., and Pérez, F. (2019). Post-fire response of *Araucaria araucana* (Molina) K. Koch: assessment of vegetative resprouting, seed production and germination. *Gayana. Bot.* 76, 119–122. doi: 10.4067/S0717-66432019000100119

Fuentes-Ramirez, A., Barrientos, M., Almonacid, L., Arriagada-Escamilla, C., and Salas-Eljatib, C. (2018). Short-term response of soil microorganisms, nutrients and plant recovery in fire-affected *Araucaria araucana* forests. *Appl. Soil Ecol.* 131, 99–106. doi: 10.1016/j.apsoil.2018.08.010

Fuentes-Ramirez, A., Salas-Eljatib, C., González, M. E., Urrutia-Estrada, J., Arroyo-Vargas, P., and Santibañez, P. (2020). Initial response of understorey vegetation and tree regeneration to a mixed-severity fire in old-growth *Araucaria-Nothofagus* forests. *Appl. Veg. Sci.* 23, 210–222. doi: 10.1111/avsc.12479

Garreaud, R. D., Alvarez-Garreton, C., Barichivich, J., Boisier, J. P., Christie, D., Galleguillos, M., et al. (2017). The 2010–2015 megadrought in Central Chile: impacts on regional hydroclimate and vegetation. *Hydrol. Earth Syst. Sci.* 21, 6307–6327. doi: 10.5194/hess-21-6307-2017

González, M., Cortes, M., Izquierdo, F., Gallo, L., Echeverría, C., Bekkesy, S., et al. (2006). "Araucaria araucana" in Las especies arbóreas de los bosques templados de Chile y Argentina. Autoecología (Valdivia: Marisa Cuneo Ediciones), 36–53.

González, M. E., Muñoz, A. A., González-Reyes, Á., Christie, D. A., and Sibold, J. (2020). Fire history in Andean *Araucaria-Nothofagus* forests: coupled influences of past human land-use and climate on fire regimes in North-West Patagonia. *Int. J. Wildland Fire* 29, 649–660. doi: 10.1071/WF19174

González, M. E., and Veblen, T. T. (2007). Incendios en bosques de Araucaria araucana y consideraciones ecológicas al madereo de aprovechamiento en áreas recientemente quemadas. *Rev. Chil. Hist. Nat.* 80, 243–253. doi: 10.4067/S0716-078X2007000200009

González, M. E., Veblen, T. T., and Sibold, J. S. (2010). Influence of fire severity on stand development of *Araucaria araucana-Nothofagus pumilio* stands in the Andean Cordillera of South-Central Chile. *Austral Ecol.* 35, 597–615. doi: 10.1111/j.1442-9993.2009.02064.x

Harvey, B. J., Donato, D. C., and Turner, M. G. (2016). Burn me twice, shame on who? Interactions between successive forest fires across a temperate mountain region. *Ecology* 97, 2272–2282. doi: 10.1002/ecy.1439

He, T., Lamont, B. B., and Pausas, J. G. (2019). Fire as a key driver of earth's biodiversity. *Biol. Rev.* 94, 1983–2010. doi: 10.1111/brv.12544

Johnstone, J. F., Allen, C. D., Franklin, J. F., Frelich, L. E., Harvey, B. J., Higuera, P. E., et al. (2016). Changing disturbance regimes, ecological memory, and forest resilience. *Front. Ecol. Environ.* 14, 369–378. doi: 10.1002/fee.1311

Kassambara, A., Kosinski, M., Biecek, P., and Fabian, S. (2021). Survminer: drawing survival curves using "ggplot2" (version 0.4.9). Available online at: https://cran.r-project.org/web/packages/survminer/index.html (Accessed April 4, 2025)

Keeley, J., Pausas, J., Rundel, P., Bond, W., and Bradstock, R. (2011). Fire as an evolutionary pressure shaping plant traits. *Trends Plant Sci.* 16, 406–411. doi: 10.1016/j.tplants.2011.04.002

Kelly, L. T., Fletcher, M.-S., Oliveras Menor, I., Pellegrini, A. F. A., Plumanns-Pouton, E. S., Pons, P., et al. (2023). Understanding fire regimes for a better Anthropocene. *Annu. Rev. Environ. Resour.* 48, 207–235. doi: 10.1146/annurev-environ-120220-055357

Kitzberger, T., Perry, G. L. W., Paritsis, J., Gowda, J. H., Tepley, A. J., Holz, A., et al. (2016). Fire-vegetation feedbacks and alternative states: common mechanisms of temperate forest vulnerability to fire in southern South America and New Zealand. *N. Z. J. Bot.* 54, 247–272. doi: 10.1080/0028825X.2016.1151903

Köbel, M., Listopad, C. M. C. S., Príncipe, A., Nunes, A., and Branquinho, C. (2021). Temporary grazing exclusion as a passive restoration strategy in a dryland woodland: effects over time on tree regeneration and on the shrub community. *For. Ecol. Manag.* 483:118732. doi: 10.1016/j.foreco.2020.118732

Lara, A., Solari, M. E., Rutherford, P., Thiers, O., Trecaman, R., Prieto, R., et al. (1999). "Cobertura de la vegetación original de la EcoRegión de los bosque valdivianos en Chile hacia 1550" in Informe técnico. Proyecto FB 49-WWF/Universidad Austral de Chile (Valdivia: Marisa Cuneo Ediciones).

Lewis, J. S., Clair, S. B. S., Fairweather, M. L., and Rubin, E. S. (2024). Fire severity and ungulate herbivory shape forest regeneration and recruitment after a large mixed-severity wildfire. *For. Ecol. Manag.* 555:121692. doi: 10.1016/j.foreco.2024.121692

Lindenmayer, D. B., Westgate, M. J., Scheele, B. C., Foster, C. N., and Blair, D. P. (2019). Key perspectives on early successional forests subject to stand-replacing disturbances. *For. Ecol. Manag.* 454:117656:117656. doi: 10.1016/j.foreco.2019.117656

Luebert, F., and Pliscoff, P. (2017). Sinopsis bioclimática y vegetacional de Chile. Santiago: Editorial Universitaria.

Marchant, C. (2019). La práctica trashumante Pehuenche en la Araucanía andina: Una forma de construir y habitar los territorios de montaña del sur de Chile. *Rev. Geogr. Norte Gd.* 74, 187–206. doi: 10.4067/S0718-34022019000300187

Marsh, C., Crockett, J. L., Krofcheck, D., Keyser, A., Allen, C. D., Litvak, M., et al. (2022). Planted seedling survival in a post-wildfire landscape: from experimental planting to predictive probabilistic surfaces. *For. Ecol. Manag.* 525:120524. doi: 10.1016/j.foreco.2022.120524

Marshall, L. A. E., Fornwalt, P. J., Stevens-Rumann, C. S., Rodman, K. C., Chapman, T. B., Schloegel, C. A., et al. (2024). What influences planted tree seedling survival in burned Colorado montane forests? *For. Ecol. Manag.* 572:122321. doi: 10.1016/j.foreco.2024.122321

McWethy, D. B., Pauchard, A., García, R. A., Holz, A., González, M. E., Veblen, T. T., et al. (2018). Landscape drivers of recent fire activity (2001–2017) in south-Central Chile. *PLoS One* 13:e0201195. doi: 10.1371/journal.pone.0201195

Miller, J. D., and Thode, A. E. (2007). Quantifying burn severity in a heterogeneous landscape with a relative version of the delta normalized burn ratio (dNBR). *Remote Sens. Environ.* 109, 66–80. doi: 10.1016/j.rse.2006.12.006

Mora, M., and Crisóstomo, R. (2016). Incendios forestales, bajo el ojo de la teledetección (Reporte Técnico 383). Santiago: CONAF, 64.

Papú, S., Berli, F., Piccoli, P., Patón, D., Ortega Rodriguez, D. R., and Roig, F. A. (2021). Physiological, biochemical, and anatomical responses of *Araucaria araucana* seedlings to controlled water restriction. *Plant Physiol. Biochem.* 165, 47–56. doi: 10.1016/j.plaphy.2021.05.005

Pausas, J. G., Bradstock, R. A., Keith, D. A., and Keeley, J. E. (2004). Plant functional traits in relation to fire in crown-fire ecosystems. *Ecology* 85, 1085–1100. doi: 10.1890/02-4094

Premoli, A., Quiroga, P., and Gardner, M. (2011). IUCN red list of threatened species: *Araucaria araucana*. IUCN red list of threatened species. Available online at: https://www.iucnredlist.org/en (Accessed November 30, 2024).

R Core Team (2024). R: A language and environment for statistical computing. Vienna: R Foundation for Statistical Computing.

Raffaele, E., Veblen, T. T., Blackhall, M., and Bucardo, N. (2011). Synergistic influences of introduced herbivores and fire on vegetation change in northern Patagonia, Argentina. *J. Veg. Sci.* 22, 59–71. doi: 10.1111/j.1654-1103.2010.01233.x

Rechene, C., Bava, J., and Mujica, R. (2003). Los bosques de Araucaria araucana en Chile y Argentina. GTZ-Deutsche Gesellschaft für Technische Zusammenarbeit. Available online at: https://www.yumpu.com/es/document/read/34361069/los-bosques-de-araucaria-araucana-en-chile-y-argentina-gtz

Rodman, K. C., Veblen, T. T., Andrus, R. A., Enright, N. J., Fontaine, J. B., Gonzalez, A. D., et al. (2020). A trait-based approach to assessing resistance and resilience to wildfire in two iconic North American conifers. *J. Ecol.* 109, 313–326. doi: 10.1111/1365-2745.13480

Rozzi, R., Armesto, J. J., Gutierrez, J., Massardo, F., Likens, G., Anderson, C., et al. (2012). Integrating ecology and environmental ethics: earth stewardship in the southern end of the Americas. *Bioscience* 62, 226–236. doi: 10.1525/bio.2012.62.3.4

Rudolphi, J., Jönsson, M. T., and Gustafsson, L. (2014). Biological legacies buffer local species extinction after logging. *J. Appl. Ecol.* 51, 53–62. doi: 10.1111/1365-2664.12187

Sanguinetti, J., Ditgen, R. S., Donoso-Calderón, S. R., Hadad, M. A., Gallo, L., González, M. E., et al. (2023). Información científica clave para la gestión y conservación del ecosistema biocultural del Pewén en Chile y Argentina. *Bosque* 44, 179–190. doi: 10.4067/s0717-92002023000100179

Sanguinetti, J., and Kitzberger, T. (2010). Factors controlling seed predation by rodents and non-native *Sus scrofa* in *Araucaria araucana* forests: potential effects on seedling establishment. *Biol. Invasions* 12, 689–706. doi: 10.1007/s10530-009-9474-8

Sayedi, S. S., Abbott, B. W., Vannière, B., Leys, B., Colombaroli, D., Gil Romera, G., et al. (2024). Assessing changes in global fire regimes. *Fire Ecol.* 20:18. doi: 10.1186/s42408-023-00237-9

Seidl, R., Rammer, W., and Spies, T. A. (2014). Disturbance legacies increase the resilience of forest ecosystem structure, composition, and functioning. *Ecol. Appl.* 24, 2063–2077. doi: 10.1890/14-0255.1

Stanturf, J. A., Palik, B. J., and Dumroese, R. K. (2014). Contemporary forest restoration: a review emphasizing function. *For. Ecol. Manag.* 331, 292–323. doi: 10.1016/j.foreco.2014.07.029

Tepley, A. J., Thomann, E., Veblen, T. T., Perry, G. L. W., Holz, A., Paritsis, J., et al. (2018). Influences of fire-vegetation feedbacks and post-fire recovery rates on forest landscape vulnerability to altered fire regimes. *J. Ecol.* 106, 1925–1940. doi: 10.1111/1365-2745.12950

Therneau, T. M., Lumley, T., Atkinson, E., and Crowson, C. (2024). Survival: survival analysis (version 3.7-0). Available online at: https://cran.r-project.org/web/packages/survival/index.html (Accessed April 4, 2025).

Torrejón, F. (2001). Variables geohistóricas en la evolución del sistema económico Pehuenche durante el periodo colonial. *Universum* 16, 219–236.

Turner, M. G., Baker, W. L., Peterson, C. J., and Peet, R. K. (1998). Factors influencing succession: lessons from large, infrequent natural disturbances. *Ecosystems* 1, 511–523. doi: 10.1007/s100219900047

Turner, M. G., Braziunas, K. H., Hansen, W. D., and Harvey, B. J. (2019). Short-interval severe fire erodes the resilience of subalpine lodgepole pine forests. *Proc. Natl. Acad. Sci. U.S.A.* 116, 11319–11328. doi: 10.1073/pnas.1902841116

Urrutia-Estrada, J., Fuentes-Ramírez, A., and Hauenstein, E. (2018). Diferencias en la composición florística en bosques de *Araucaria-Nothofagus* afectados por distintas severidades de fuego. *Gayana. Bot.* 75, 625–638. doi: 10.4067/S0717-66432018000200625

Vargas-Gaete, R., Muñoz, B., and Penneckamp, D. (2024). "Degradación de ecosistemas forestales, definiciones y conceptos aplicados a los bosques de Chile" in

Restauración de Ecosistemas Forestales. eds. J. R. Bannister, J. Ovalle, R. Vargas-Gaete and V. Claramunt-Torche (Santiago: Editorial Universitaria), 800.

Veblen, T. T. (1982). Regeneration patterns in *Araucaria araucana* forests in Chile. *J. Biogeogr.* 9, 11–28. doi: 10.2307/2844727

Whitlock, C., Mcwethy, D. B., Tepley, A. J., Veblen, T. T., Holz, A., McGlone, M. S., et al. (2015). Past and present vulnerability of closed-canopy temperate forests to altered fire regimes: a comparison of the Pacific Northwest, New Zealand, and Patagonia. *Bioscience* 65, 151–163. doi: 10.1093/biosci/biu194

Zamorano-Elgueta, C., Cayuela, L., González-Espinosa, M., Lara, A., and Parra-Vázquez, M. R. (2012). Impacts of cattle on the South American temperate forests: challenges for the conservation of the endangered monkey puzzle tree (*Araucaria araucana*) in Chile. *Biol. Conserv.* 152, 110–118. doi: 10.1016/j.biocon.2012.03.037